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CONTRIBUTIONS FROM THE ZOÖLOGICAL LABORATORY OF THE MUSEUM OF COMPARATIVE ZOÖLOGY AT HARVARD COLLEGE. E. L. MARK, DIRECTOR.—No. 155.

THE EFFECT OF HEAT ON THE COLOR CHANGES IN THE SKIN OF ANOLIS CAROLINENSIS Cuv.

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I. Introduction.

About a year ago Carlton (:**03**, p. 264) published the statements that, when a brown Anolis is put in the dark it invariably turns green in about twenty-five minutes, and when a green one is exposed to light it almost invariably turns brown in about four minutes. In attempting to ascertain what sense organs were concerned with these color changes, we repeated Carlton's experiments to determine independently the rate of change, and obtained results that were often far from uniform. Marked differences in the time required for the color changes on different days and at different times on the same day made the experiments very unsatisfactory. The change from brown to green was often slower at the beginning than after the experiments had been carried on for a few hours. This led us to suspect that one might apply to Anolis Pouchet's ('**76**, p. 73) conclusion concerning turbots: that exercise shortened the period for color changes. In fact this seemed to be confirmed by the following observations: On the morning of December 28 a set of animals was found that remained brown in the dark for three hours. Subjecting them alternately to the dark and to the light in a box provided with an electric lamp soon brought them to a state at which they would change from brown to green. This they did in an average time of 19.80 minutes, the last four records giving an average of 13 minutes. Thus it seemed that exercise played an important part in determining the rate of change.

Nevertheless, since all our experiments had been carried on with more or less change of temperature, it was necessary to check this before any sound conclusions could be drawn as to other factors. On December 30, with the temperature in the box varying from 22° C. just before the experiments were begun to 27° at the close of them, the average time of twenty records at various intermediate temperatures was 15.58 minutes, while at 27° it was 12 minutes. Therefore, notwithstanding the opinion of many investigators that temperature plays little or no part in the color changes of lizards and other lower vertebrates, we determined to test the influence of heat on Anolis, and the results obtained are given on the following pages.

II. Apparatus.

The apparatus used consisted of a wooden, upright, constant-temperature box, 70 cm. high, 35 cm. deep, and 40 cm. wide. The front of this box was in the form of a tight-fitting door, near the middle of which was a small glass window so placed that observations could be made from the outside without opening the box to the air. This window was provided with a light-proof shutter.

The interior of the box was lined with black cloth, and on the bottom was placed a cylindrical metal water-chamber 10 cm. high and 32 cm. in diameter. This held about 8 litres of water, which could be kept at constant temperature by a slow flow through an inlet and outlet connected with a water supply outside the box. On the inside of the back of the box, 45 cm. above the top of the water-chamber, was placed an electric incandescent lamp, which could be controlled from the outside by a key. About 10 cm. below this was inserted in the box a wooden cross partition carrying an oblong flat-bottomed glass dish. This contained distilled water 3 cm. deep, and served as a heat screen when the lamp was lighted. As the air of the small upper chamber which contained the lamp soon became heated when the lamp was lighted, a ventilating system was provided. This consisted of a lower inlet pipe and an upper outlet pipe, both of which had elbows in them to prevent the entrance of light. When the lamp was lighted a temperature anywhere between 10° and 50° C., and constant to within half a degree or so, could be easily maintained at the level of the top of the water-chamber. This was shown by a thermometer inserted through the wall of the box at this point.

It was found on trial that the nervous states of the lizards had much to do with the rate of the color changes, and to get uniform records it was necessary to keep them as nearly in one state in this respect as possible. Since the lizards chase one another when together, and thus introduce disturbing factors, each one was placed in a small oblong box painted black inside and resting directly on the top of the water-chamber; each box was covered by a plate of glass. When the light was turned on, the rays, after passing through the heat screen and the glass top of the small box, fell upon the lizard with an intensity of about 115 candle-metres. The top of the water-chamber was large enough to allow six lizards to be experimented upon at once, and that number was usually employed.

III. Experiments.

From what has already been stated by Carlton (:**03**) it is evident that in testing the effect of temperature changes on Anolis it is necessary to exclude light, or at least to control it so that its influence will not enter into the final result. The constant-temperature box, already described, was planned with this in view.

Our first experiments were designed to determine the rate of change from brown to green at different temperatures. For this purpose six lizards were placed, one in each of the six small boxes on the water-chamber, and after the whole apparatus had come to the requisite temperature the rate of change was ascertained in the following way: The incandescent lamp was lighted and the lizards were kept under its influence until they were thoroughly brown. Then the light was turned out, and the length of time needed for the change to green was recorded for each individual. To ascertain when this had occurred the box was from time to time momentarily illuminated by the lamp and an observation was made through the small glass window. As a rule, four such determinations on each of six animals were made for each temperature, so that in the following table the average time for a given temperature is based on twenty-four records.

Table I shows the average rates at which these lizards changed from brown to green at temperatures ranging from 10° C. to 45° C.

At 10° the animals remained brown in the dark as well as in the light. Hence at this temperature heat was the controlling factor.

At 20° the animals slowly changed to green. Since at this temperature they remained brown in the light, it is evident that the change to green is not dependent upon heat, but upon the absence of light. That the heat, however, had some influence at this stage is seen from the fact that the change to green was very slow, the heat at 20° almost counteracting the change that takes place as the result of darkness.

At 25° the animals changed more quickly to green than at 20°, showing that at a higher temperature the heat had less retarding effect. The same was true, but still more noticeably, at 30°.

At 35° the heat checked the coming on of the green more than at 30° or even 25°, though the condition at 35° was followed by stages (40° and 45°) at which the animals were persistently greenish even in the light. Why retardation should occur at 35° is not clear, for one would expect a still more rapid rate than at 30°. However, subsequent tests of this invariably showed that the rate was persistently slower at 35° than at 30°, and hence we cannot conclude that this record was due to faulty observation. Possibly the increase of temperature which between 20° and 30° may have acted on the melanophores of the skin in one way, e. g., directly, may at 35° have influenced them in another way, e. g., indirectly through nerves. But to this question we have no definite answer.

TABLE I.

Rate of Change of Anolis from Brown to Green at Different Temperatures.

Temperatures in Degrees Centigrade.	Average Time in Minutes to change from Brown to Green.	
	In the Dark.	In the Light.
10	Remained brown.	
20	19.66	Remained brown
25	13.23	" " "
30	10.93	" " "
35	15.48	" " "
40	Greenish gray.	
45	Greenish gray to green.	

At 40° and 45° the animals became greenish and remained persistently so. As this happened not only in the dark but also in the light, where we might have expected the animals to have remained brown, it follows that at these temperatures heat was again a controlling stimulus preponderating over light.

Since at 40° and 45° the animals were persistently green, or at least greenish, it was impossible by the method we adopted for using the constant-temperature box to get records of rates comparable with those for the temperatures 20° to 35°. As a means of ascertaining roughly what the rate was at high temperatures four animals were put in a muslin-covered cage, and after they had become thoroughly brown in the light, the cage and they were quickly transferred to the dark, constant-temperature box at 54°. In six minutes two of the lizards were green and two yellowish-green. In a second trial with the box at 58° the change to green was accomplished in a little over four minutes. In both these trials the necessity of opening the box to the outer air and the conditions under which the lizards were exposed to the heat inside made it impossible to state exactly what the temperature was that induced the change. It must, however, be evident that at these higher temperatures the rate is more rapid than at those recorded in Table I, and this is what was to be expected.

TABLE II.

Rate of Change of Anolis from Green to Brown at Different Temperatures.

Temperatures in Degrees Centigrade.	Average Times in Minutes to change from Green to Brown.	
	In the Dark.	In the Light.
10	Brown.	
20	Remained green	4.23
25	“ “ “	3.52
30	“ “ “	3.13
35	“ “ “	2.80
40	Remained greenish gray.	
45	Remained greenish gray to green.	

The effects of heat on the change from green to brown has also been worked out, as in the case of the opposite change, and the results are given in Table II.

At 10° the animals became brown, and, as in the former records at this temperature, they remained so, irrespective of illumination. Their rate of change at this temperature could not therefore easily be determined. Green animals, however, when introduced into the dark, constant-temperature box changed to brown in about 18 minutes, but this record, which was obtained only after opening the box and handling the animals, can be regarded as only approximate. Its slowness is doubtless due to the circumstance that it represents a conflict between two opposing conditions: dark, inducing the green state, and low temperature, inducing the brown one; for when green lizards were introduced into the lighted box at 10° they changed to brown in 2.55 minutes.

From 20° to 35° the green animals when in the dark remained green, a condition determined not by temperature but by the absence of light, for when they were exposed to light at these temperatures they changed to brown at ever-increasing rates from 4.23 seconds at 20° to 2.80 seconds at 35°. Although heat between 20° and 35° is no more the controlling factor in the change from green to brown than it is in the reverse change (Table I), its influence is seen in the increased rate of the change, characteristic of the range from 20° to 35° under uniform illumination.

At 40° and 45° green animals, as might have been expected, remained green or greenish gray, irrespective of the illumination.

From these two sets of records it is evident that at a low temperature (10°) the lizards change from green to brown but not the reverse, and remain brown irrespective of illumination (115 candle-metres). At high temperatures (40° and 45°) they turn from brown to green but not the reverse, and remain green or greenish irrespective of illumination (115 candle-metres). Between these two extremes, at both of which heat is the controlling factor, there is a range (20° to 35°) through which light is the controlling factor, though heat here is not without its influence. This is indicated by the differences of rate in the changes from brown to green (Table I) and green to brown (Table II), accompanying the differences of temperature.

Thus it is well established that the rate of the color changes in Anolis is always more or less influenced by temperature, and the discrepancies between our early results and those of Carlton undoubtedly depended chiefly upon this factor, for Carlton's experiments were carried on in a room that throughout the winter retained a rather high uniform temperature (18° to 20°), whereas ours were begun in one whose temperature was subject to much variation.

Before turning to a general discussion of our results comment should be made on the bearing of these conclusions on certain conditions observed in Anolis under natural surroundings. Judging from their reactions to light as recorded by Carlton (:**03**), we should expect these animals in their native haunts to be brown in the daytime and green at night. We have never had the opportunity of studying Anolis in the field, but through the kindness of Dr. Caswell Grave we have been informed that in the neighborhood of Beaufort, N. C., on a hot, sunny day about as many green animals may be taken in bright sunshine as brown ones. This is in all probability a mixed reaction, in that some of the animals are more sensitive to light than to heat and hence turn brown in bright sunlight, and others are more sensitive to heat than to light and hence turn green under like conditions.

IV. Discussion of Results.

The brown state in Anolis, which corresponds to the dark gray or black state of many fishes, amphibians, and other reptiles, is dependent upon the accumulation of pigment in the fine peripheral branches of the melanophore cells of the derma. The green state, on the other hand, is possible only after this pigment has withdrawn into the body of the melanophore cell. We may therefore conclude that a low temperature, such as 10°, induces a migration of the pigment toward the periphery and a high one (40° or 45°) a migration toward the centre.

Thus far very few records of the migration of the pigment of chromatophores in relation to temperature have been published, but such as have appeared support the conclusions just stated, and suggest for them a much broader application. Thus it seems clear that in the African chameleon the melanophores draw in their pigment and the skin becomes light when the animal is subjected to heat, for Brücke, though he ('**51**, p. 804) declared that dark heat rays had no effect in changing the color of the skin, stated ('**52**, p. 26) that when the animal was put in an atmosphere that warmed its skin to 30° it became lighter colored. Moreover this observation was confirmed by Keller ('**95**, p. 129), who observed that when a chameleon was subjected to heat at 30° to 38° it took on a lighter tint than usual and retained this even under strong illumination, where it would be expected to become dark.

Biedermann ('**92**, p. 487), who experimented on the chromatophores of frogs and tree-toads, fully confirmed the earlier observations of Hering ('**69**, p. 53) to the effect that in cold water the pigment of the melanophores passed out into the cell processes, producing a dark skin, and in warm water it passed back into the body of the cell, leaving the skin light. Similar results have been more recently obtained on larval salamanders by Fischel ('**96**), and these have been confirmed by Flemming ('**97**^{a}, **97**^{b}).

Thus all recorded cases support the generalization that a high temperature induces a migration of the pigment into the body of the cell, and a low one the reverse. Wiedersheim (see Hoffmann, '**90**, p. 1353), therefore, was not without reason in suspecting that the dark skin of Phrynosoma on cool, cloudy days, and its pale skin on sunny days might be due to temperature differences, and Keller's ('**95**, p. 132) criticism of this explanation is at least premature. It must, however, be admitted that, as Thilenius ('**97**, p. 536) has pointed out, light is usually more effective than heat as a chromatophore stimulus, though to deny heat any part in the determination of color changes is, as our results show, certainly erroneous.

The relations of heat to light in these respects are not without interest. Thus while heat seems in all cases to follow the simple rule that high temperature induces a central migration and low temperature a peripheral migration of the melanophore pigment, light sometimes follows this rule and at other times does not. For in Veranus, Uromastix, and Agama (Thilenius, '**97**), a strong light acts like a high temperature and inducing central migration, and a dim light or no light acts like a low temperature and inducing peripheral migration. On the other hand, in the African chameleon (Brücke, '**52**; Keller, '**95**, etc.), and in Anolis (Carlton, :**03**) a strong light acts like a low temperature, inducing a peripheral migration, and a dim light or no light acts like a high temperature, inducing a central migration. In other words, in the first group of animals mentioned light and heat act together; in the second, they are antagonistic. Whether there are animals which react to heat in the reverse way, — high temperature causing in them a peripheral migration of pigment, — as some do to light, remains still to be made out, but from our present knowledge it seems probable that this is not true, and furthermore that animals are much more differentiated toward light than toward heat, even though from a physical standpoint these two stimuli have much in common.

V. SUMMARY.

1. At 10° C. Anolis carolinensis becomes brown and remains so, irrespective of illumination (115 candle-metres). At this temperature heat is the controlling factor.

2. At 40° and 45° C. Anolis becomes green or greenish-gray, and remains so irrespective of illumination (115 candle-metres). Here also heat is the controlling factor.

3. At intermediate temperatures, 20° to 35°, light (115 candle-metres) and dark are controlling factors, but the effect of heat is still evident over this range in that it may influence the rate of the color changes.

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